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AN ECOLOGICAL STUDY OF THE LIFE-HISTORY OF THE FRESH-WATER ATHERINE FISH LABIDESTHES SICCULUS[1]

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CONTENTS

INTRODUCTORY 262
COMPLEMENTARY DISTRIBUTION OF ADULT AND YOUNG 263
1. Habitat selection of young 263
2. Habitat selection of adults 263
3. Basis of complementary distribution 264
HABITS 267
4. Habits of adults by day and at night 267
5. Habits of young 268
6. Correlation between habits and structures 269
7. Breeding habits 270
LIFE-HISTORY 271
8. The egg 271
9. Rate of development of young 272
10. The life-cycle of Labidesthes 274

INTRODUCTORY

This paper is one of several which the writer hopes to prepare, dealing with the general environmental relations of a particular fish species during the various stages in its life-cycle; with diurnal, seasonal and age changes in its habits and in habitat reactions, with the varied effects of the environment on its rate of growth, and with the main features of its life-history. The material for the present study was largely obtained during the summer of 1920, when the writer made an ichthyological survey[2] of Portage Lake and adjacent waters, of the Huron River basin in southeastern Michigan. The species treated here is *Labidesthes sicculus* Cope,—the only strictly fresh-water representative of the acanthopterygian family Atherinidae in the United States, and the only species of a rather aberrant genus;[3] a species occurring, with local abundance, in the lakes and in those portions of streams most lake-like ecologically, from the basin of the lower Great Lakes southward to Florida and Texas.

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[1] T. L. Hankinson, Jacob Reighard and Lee R. Dice have kindly read the manuscript for this paper.

[2] For the Michigan State Geological and Biological Survey.

[3] Concerning the systematic position and relationships of this fish, see Jordan and Hubbs, "A Monographic Review of the Family of Atherinidae or Silversides" (Stanford Univ. Publ.), 1919, pp. 1–87; 11 pls.

COMPLEMENTARY DISTRIBUTION OF ADULT AND YOUNG

Perhaps the most sharply outstanding feature of the environmental relations of Labidesthes is the remarkable difference in habitat selection displayed by the very young and the adults; a phenomenon which apparently has barely been noticed.

1. HABITAT SELECTION OF YOUNG.—The young of *Labidesthes sicculus* soon, probably immediately, after hatching on the shoals of the inland lakes studied, were found to leave the shallow waters, moving outward to assume a pelagic habitat over deep water.[4] These very young fishes comprised indeed the only characteristic fish element in the limnetic community of these lakes. Only rarely during the first month of their existence were the young seen to return over shoal waters, although repeatedly and carefully sought for there:[5] they were found to become gradually fewer as one came onto a shoal gently sloping into deep water,[6] few individuals straggling into water shallower than one meter. Often they were most abundant in Portage Lake over its deepest portion (20 to 26 meters). In the Huron River, a stream of rather small size yet in part very deep in the vicinity of Portage Lake, the young of Labidesthes occurred over the quieter stretches away from the shores, most abundantly over the deepest available water. In a smaller stream of the same system, rather thoroughly explored, the very young were located only in the widest and deepest pool of its lower course.

As these young fishes rapidly grew during the summer, they showed less aversion to shoal waters. Although the work at Portage Lake was discontinued early in August, it is thoroughly evident from the data accompanying specimens from this locality and from harbors and estuaries about Lake Erie, from published records, and especially from detailed observations made during October in Whitmore Lake, near Portage Lake, that during August and September the young of *Labidesthes sicculus* return to shallow water; at first intermittently, but soon permanently.[7] During the winter, Evermann and Clark (l.c.) found Labidesthes close to the shore, beneath the ice.

2. HABITAT SELECTION OF ADULTS.—In striking contrast to this preference for a limnetic habitat displayed by the very young of Labidesthes in the

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[4] Evermann and Clark (Lake Maxinkuckee, 1920, p. 376) briefly record observing schools of very young Labidesthes over the deep water of an Indiana lake.

[5] Observation was rendered particularly easy and conclusive by the surface swimming habits of these fishes.

[6] At times an actual concentration of these young fishes was noticed over the outer edge of shoals having an abrupt outer slope.

[7] Evermann and Clark (Lake Maxinkuckee, 1920, pp. 240–251) record taking many Labidesthes, mostly young, on the shoals of Lake Maxinkuckee in July, 1899. Later (p. 378) they mention that these may have been young of the year before. This statement, in view of the life-cycle of the species here made known, rather indicates that most of the specimens taken were adults.

lakes studied, the adults showed a practically exclusive selection of the shoal community: they were found generally distributed and in moderate abundance over the shallow waters, even as far as 0.4 km. from the shore where a marl shoal extended out to the middle of a small lake. Only rarely was an adult observed[8] more than a few meters beyond the outer edge of a shoal terrace; not once was one seen over deep water toward the middle of a lake (where the young, as above mentioned, were frequently most abundant), nor about the small marl shoals disconnected from the shoals about the shore. In the Huron River, the adults occurred in greatest concentration in water shallower than one meter; in most places, however, showing no apparent preference toward—nor avoidance of—the actual shore-line, frequently occurring in the center of the stream. In this laterally restricted river community the habitats selected by the very young and the adults, while differing in average and in extreme, widely overlapped, but in the lakes were more sharply opposed one to the other. In brief, the associational distribution of the young shorter than about 25 mm. and the adults was sharply complementary.

3. BASIS OF COMPLEMENTARY DISTRIBUTION.—The causal explanation of this remarkable difference in selection of habitat by the very young and the adult of *Labidesthes sicculus* presents an interesting ecological problem, toward the solution of which the writer can now offer an imperfect suggestion, after having made a partial analysis of the factors involved. Only lake conditions will be considered,[9] and remarks will be further confined to Portage Lake. Of several possible factors more or less thoroughly studied in this lake, the following will be briefly discussed in this order: temperature, light, oxygen, food, seclusion from enemies, and reactions.

A. Temperature may definitely be eliminated as a factor controlling the associational distribution of Labidesthes. The very young occur almost exclusively over deep water, the adults almost exclusively over the shoals, by day as well as by night, despite the fact that in the normal diurnal temperature cycle of the summer, the shallow water is cooler at night and in the early morning, and warmer during most of the day, than are the open waters of the same lake. Of the detailed records which bear on this point, only those of a single morning, being typical of all, need be given: over a marl shoal where the young rarely straggled, though adults were often present, the temperature was raised from 20.85° C. at 7:15 A.M. to 21.85° at 9:15; at the edge of the same shoal, where a few young were noted, the temperature change during approximately the same interval was from 21.40° to 21.80°; over deep water, where the young were everywhere abundant, but the adults always absent, the rise in temperature was from 21.00° and 21.20° (two situations) to 21.70° C.

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[8] Again it should be recalled, that, as made clear in the account of its habits given later, this species swims consistently at or very near the surface: a fact rendering particularly significant the often repeated observations made by the writer on its associational distribution.

[9] It must be recalled, however, that Labidesthes belongs to a family essentially marine. It is therefore possible that its habitat-reactions were inherited from its marine ancestors, and hence were developed in the sea.

B. Light can scarcely be a factor determining the differential distribution of these two stages in the life-cycle of Labidesthes, for both the very young and the adult habitually remain at or very near the surface of the water where they are similarly subjected to intense illumination during the day. Furthermore, a greater range of light conditions obviously prevails over the shoals than over the deep water.

C. A series of oxygen analyses[10] made by the writer in Portage Lake (a lake of the second class), and in Mud Bay, nearly disconnected from it (and really a lake of the third class), makes it appear highly improbable that the amount of dissolved oxygen over the shoals and the deep water causes the selection of these habitats respectively by the adults and the very young of Labidesthes. In situations where the young were absent the oxygen content varied from 4.50 to 7.11 cc. per liter (average of six analyses, 5.80 cc.); in situations where the young were abundant, the oxygen content varied from 5.44 to 6.14 cc. per liter (average of six analyses, 5.92 cc. per liter).

D. Although the food of *Labidesthes sicculus* has been rather thoroughly studied by Forbes,[11] Forbes and Richardson,[12] Pearse, [13] Baker,[14] and Evermann and Clark,[15] and the published analyses are not of critical significance in the present connection, because most of the specimens examined were young-of-the-year obtained in late summer after their invasion of the shoal waters: the records deal chiefly neither with the very young living over deep water, nor with the adults over the shoals (the two stages under consideration). These authors found the food of Labidesthes to consist largely of such aquatic and land insects as occur at the surface of the water, and of entomostracans, the insects somewhat predominating. This mixed diet is used, then, during an intermediate stage in the life-cycle of the species. The very young obtained by the writer over deep water had fed almost exclusively on plankton crustaceans; as they grew they gradually began to prey on the insects which abound at the surface during the summer; the mature fishes had fed almost entirely on insects. This approximately synchronous change in food- and habitat-selection suggests a causal relation; but some observations are inconsistent with the suggestion. As Evermann and Clark have noted, they often feed chiefly on entomostraca even after entering shoal waters. Plankton in Portage Lake was found to be especially abundant over certain plant-overgrown shoals, abruptly avoided by the plankton-feeding young; insects (small Chironomidae in particular) emerged in abundance over the whole surface of Portage Lake in midsummer, though the insect-eating adults remained on the shoals. It seems safe to conclude that food it not determinately involved in the complementary distribution of the very young and the adults of Labidesthes.

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[10] Directions for the analysis of dissolved oxygen by Winkler's method are given by Birge and Juday (Bull. Wisc. Geol. and Nat. Hist. Surv., 22, 1911, pp. 5–21). It is advisable, however, to alter somewhat details of method, and necessary to do so if much organic matter is dissolved in the water. Winkler has given revised directions which seem to have escaped the attention of ecologists (see Zeit. Anal. Chem., 53, 1914, pp. 665–672, and Lunge u. Berl's Chemisch-technische Untersuchungsmethoden, Bd. 2, 1910, pp. 279–281. A modification of Winkler's method is given in the standard methods for the examination of water and sewer, 4 ed., 1920, pp. 65–68 (prepared by American Public Health Association).

[11] Bull. Ill. Lab. Nat. Hist., no. 2, 1878, pp. 78, 84, 88, 89; ibid., no. 6, 1883, pp. 69, 70, 93; ibid., Vol. 2, 1888, pp. 479, 502, 514–532.

[12] Nat. Hist. Surv. Ill., Vol. 3, 1908, p. 228.

[13] Bull. Wisc. Nat. Hist. Soc., 12, 1915, pp. 16, 17; Bull. U. S. Bur. Fish., 35, 1915–1916 (1918), pp. 262, 263, 278, 284.

[14] Bull. Syracuse Univ., 16, 1916, pp. 180, 181 (table opp. p. 212), 296, 299; ibid., 18, 1918, p. 216.

[15] Lake Maxinkuckee, 1920, pp. 296, 378.

E. The protection afforded the very young of Labidesthes during the critical newly hatched stage by their relative seclusion from predaceous small fishes, in their habitat over deep water, is probably correlated fundamentally with their selection of this habitat (some young Labidesthes which had wandered over the edge of a shoal were observed preyed upon by the young-of-the-year of *Micropterus salmoides*). But the avoidance of the shoals by these young of Labidesthes can not be immediately determined by any such factor, for the young fishes were often found avoiding the shoals, even though no other animals were in evidence. And certainly seclusion from enemies can not explain the invasion of the hoals by these young silversides in late summer, nor the exclusive presence there of the adults.

G. From the foregoing it appears probable that neither such physical factors[16] as temperature, light or oxygen, nor such biological factors as food or seclusion from enemies, are determinately involved in the selection by the very young of Labidesthes of a habitat over deep water. Supported by this negative evidence, some positive indications suggest that the causal factor is a strong negative response, presumably visual, to the presence of large objects. The reaction of the very young of *Labidesthes sicculus,* and in comparison those of the very young of *Notropis cornutus* and of *Notropis hudsonius,* toward a slowly moving or stationary boat were noted on many occasions. The very young of these two species of "shiners," which occurred in great abundance and almost exclusively about the very shoreward margin of the water, moved rapidly toward the boat, about which they soon clustered in large schools. The very young of Labidesthes, living over deep water beyond the shoals, on the contrary almost invariably swam rapidly and directly away from the boat. As these species grew, however, their response to the presence of the boat gradually became notably less contrasted: the young of the two species of Notropis became less closely restricted to the shore-line, remaining by day in the more open waters of the shoals, and often venturing at night outward considerably beyond the shoal-slopes; while the young of Labidesthes showed less avoidance of the shoals. These field observations on the relation of the reactions to the habitat selection of Labidesthes offer a promising suggestion for experimental study.

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[16] Mr. T. L. Hankinson has suggested to the writer that the uniformity of physical conditions prevailing over deep water may determine the selection of the limnetic habitat by the sensitive young of Labidesthes. The writer does not regard the range of conditions on the shoals as wide enough in itself to cause the avoidance shown by the young toward shallow water. At least, such a factor can not be regarded as an immediate one.

HABITS

In the preceding discussion of the ecological relations of the young and the adults of *Labidesthes sicculus,* their horizontal associational distribution has been stressed. In the following account of their habits, their vertical distribution will be emphasized.

4. HABITS OF ADULTS BY DAY AND AT NIGHT.[17]—During daylight the adults were observed to swim about freely either in mid-water, or, more abundantly, near or at the surface of the water; most frequently over earthy bottom, yet often over shoals densely covered with Chara or Potamogeton, or about the edge of bulrush belts. Perhaps the most incessantly active of the fishes in the lakes studied and the most rapid in their movements, they frequently leaped out of the water and through the air in a low graceful arch, at times for distances at least ten times their own length, somewhat after the manner of the smaller, weaker flying fishes. Occasionally such a skip was repeated from one to four times, before the fish finally dove out of sight; not infrequently it seemed to occur without apparent reason, as though the fishes were at play; but the habit was also observed to serve purposeful ends, escape from a preying fish (probably a black bass), and securing of insect food. Skipping is also involved in the breeding behavior, as described later.

In striking contrast to this intense activity by day, the adults at night[18] were observed[19] to lie quiescent as though asleep (as were also adult gars,

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[17] Beyond observations that Labidesthes remains near and feeds at the surface and that it frequently skips through the air, nothing has been published concerning the habits of this fish.

[18] It is doubtless during this nocturnal period of inactivity that Labidesthes is preyed upon by mud-puppies (*Necturus*) in lakes where this salamander abounds (cf. Evermann and Clark, Proc. Ind. Acad. Sci., for 1916, pp. 501, 505). In a later paper based on the same work (Lake Maxinkuckee, 1920, p. 377), the same authors, in listing its fish and bird enemies, claim that this fish escapes the water-dog.

[19] With the aid of a cap-light, during July. Professor Pearse kindly notes that he has observed Labidesthes at the surface during November and December nights.

Lepisosteus osseus),[20] most frequently against the surface of the water, rarely on the bottom. They usually took alarm at the near approach of a moving object, darting, after an initial splash at the surface, for a distance of one to several meters, where they remained in a more readily disturbed rest. A number of other fishes of the region, for example *Percina caprodes,* were found to possess a similar contrast between their day and night habits, but normally rested on the bottom, rather than against the surface.

HABITS OF THE YOUNG.—The very young of *Labidesthes sicculus,* probably immediately after hatching[21] from the egg, came to the surface, where they swam about throughout both day and night, with their depressed head in persistent contact with the surface film. As they grew larger, particularly when the surface was roughened by storm, they tended to swim about more freely, descending as far as half a meter below the surface, yet remaining most abundant in the uppermost two decimeters of water. From the first, and throughout the limnetic existence of their first summer, as well as during their life on the shoal in the following autumn[22] and spring, and rarely during the second summer, they moved about in rather compact schools of varying size during the hours of bright daylight; but at night they occurred in loose disconnected aggregations and exhibited no definite schooling tendencies whatsoever: on the contrary they moved about singly, at the same relation to the surface as by day. Schooling was determined to be a characteristically daylight phenomenon also in the cases of the following other species of fishes of Portage Lake or their life-stages: *Erimyzon sucetta* (young-of-year); *Pimephales notatus* (young-of-year, half-grown and adults); *Notemigonus crysoleucus* (young-of-year and probably adults); *Notropis blennius* (adults); *Notropis hudsonius* (young-of-year and probably adults); *Notropis cornutus* (young-of-year); *Micropterus dolomieu* (young-of-year); *Micropterus salmoides* (young-of-year); *Perca flavescens* (young-of-year and probably adults); and *Percina caprodes* (young-of-year and adults).

The juvenile habits gradually become modified into the adult habits in the fall, when the young permanently take up their residence on the shoals. At first the skipping is very feeble, the fishes scarcely more than breaking the surface, or " lisping," as Evermann and Clark put it.

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[20] That the gars occasionally prey upon the silversides at night was determined by a study of the food of the gars taken in Portage Lake and adjacent waters. Pearse similarly lists Labidesthes among the animals eaten by the gar.

[21] The only other fish of the same waters possessing similar habits and form, namely, *Fundulus notatus,* was found to pass through a brief and transitory initial free-swimming stage among water plants in very shallow water, prior to the assumption of surface swimming habits. Richardson (Bull. Ill. St. Lab. Nat. Hist., 9, 1913, p. 421) has published a brief note on the swimming habits of young Labidesthes.

[22] Evermann and Clark (Lake Maxinkuckee, 1920, 378), claim that these fishes begin to school with the advent of cold weather. They probably do congregate in larger schools then.

6. CORRELATIONS BETWEEN HABIT AND STRUCTURE.—Many of the structural and form characters of Labidesthes and related genera are clearly correlated with these swift-swimming habits: with vigorous propulsion, and with the preservation of equilibrium and sharp control of direction in rapid locomotion. The caudal fin is rather strong and deeply forked; the spinous portions of the vertical fins are reduced, but the keel-like soft-rayed portions are moderately elevated, stiff yet thin, and falcate in outline; the pectoral fins are set high on an oblique base, and are falcate; the pelvic fins are inserted more posteriorly than in the typical acanthopterygian fishes. The myotomes (and of course the vertebrae) are increased in number, the scales reduced in size and in complexity of structure; the urosome elongated and the abdomen abbreviated, without a consequent reduction of the air-bladder, which in compensation is extended backward into the urosome.[23] Analogous modifications of structure characterize other swift-swimming surface-inhabiting genera or families of fishes derived from the Acanthopterygii.

It must be noted, however, that the contours of *Labidesthes* and of other genera of the subfamily Atherinopsinae to which it belongs, notably *Thyrina,* diverge rather widely from those of the stream-line form of least resistance to forward locomotion, which, as has been satisfactorily determined, characterizes most free-swimming animals. This divergence in form, significantly, is not in any of the varied directions taken by the many diversely shaped types of bottom fishes. The body, as in several not directly related surface-swimming members of the Poeciliidae, is in outline an elongate parallelogram, the dorsal profile anteriorly being flattened (in the frontal as well as the sagittal plane), permitting the top of the head to be applied to the surface film; while the urosome is bent downward, so that at the same time the caudal fin remains a little below the surface, in an efficient position for its sculling movements.

Similarly, the coloration of Labidesthes closely agrees with that of most other free-swimming fishes, which has certainly been correctly interpreted as having a high concealing value. The body is definitely counter-shaded; lustrous greenish or olive on the back, grading into silvery on the belly. As in a number of other, unrelated genera of shore-pelagic fishes (mostly marine), all of which seem to agree closely in habits, a more or less sharply defined lateral silvery band is developed.

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[23] That a number of these characters appear to be reversions toward the primitive condition of malacopterygian fishes is an expression of the little-emphasized fact that the main line of evolution in fishes—by some termed "ichthyization"—has been correlated with the gradual assumption of a closer ecological relation with the bottom; reversion to a more generalized free-swimming habit has been accompanied by structural reversions. Evidence that the Atherinidae are derived from typical acanthopterygian fishes, and therefore that they are not, as formerly usually held, transitional between the soft-rayed and the spiny-rayed teleosts, has been given by Jordan and Hubbs in *A monographic review of the family of Atherinidae or silversides* (Stanford Univ. Publ., 1919).

Finally, as Dr. S. A. Forbes[24] has pointed out, there exists a close correlation between the alimentary structures of Labidesthes and its feeding habits and food. The gill-rakers are long and close set, serving as a strainer for the plankton crustacea and small insects, the animals most preyed upon. The intestine is short, as in so many other carnivorous animals. Also, the prolongation of the antorbital portion of the head into a moderate beak[25] is correlated with the exclusively predaceous feeding habits of Labidesthes.

7. BREEDING HABITS.—The breeding activities of *Labidesthes sicculus* during the comparatively cool season of 1920 were found at their height in the last of May and during the first part of June,[26] or, in more significant expression, after the surface waters had been heated above 20° C. (see figure 1). For a few days following June 20 there intervened a temporary cessation of breeding activities (as similarly in the case of *Lepomis incisor*), doubtless caused by a drop in the temperature of the water at that time below 20°. With the rising temperature following this cold period breeding was resumed, and continued with decreasing intensity at least into the month of July. Indeed, unspent females with ova mature were taken as late as July 19 and 25, although no breeding activities were observed so late in the season, and the last newly hatched young were seen on July 16 and 26. Spawning occurred in the shoals of the lakes studied and in the Huron River; the most densely populated breeding area was in the moderate current

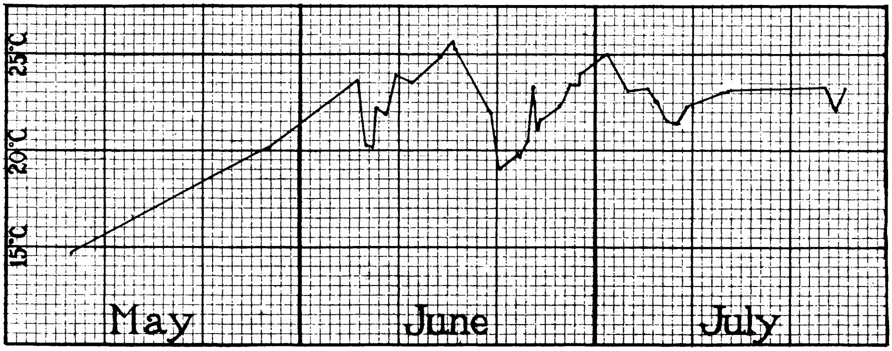

FIG. 1. Surface temperature in 1920, over the deep water of Portage Lake, Washtenaw and Livingston Counties, Michigan.

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[24] See references in footnote 10.

[25] A similar beak is developed in the Argentine atherine genus Odontesthes, the food of which is unknown.

[26] Evermann and Clark state that "the Skipjack probably spawns during the latter part of June and July."

of the river, over a washed gravel bottom at a depth of 0.3 to 1.0 meter, where the river entered one of the lakes in its course.

Particularly after the height of the breeding season, the males in these spawning areas were shown by frequently repeated observation greatly to outnumber the females.[27] Single males were at all times numerous here, but the only females observed were paired with from one to several males. Each male appeared to command a rather ill-defined area of surface water, in moderate current two to four meters long by one or two meters wide. From this area each guardian male vigorously drove off invading males, returning later, though not invariably, to approximately the same spot. During the height of the breeding activities, however, no such areal restriction of individuals was apparent, for most or all of the males as well as the females were engaged in their wild spawning.

Apparently upon entering the spawning area, the females were quickly recognized[28] as such by the males, who gave chase. The female in all cases first made away at high speed very closely pursued by one to several males. Usually she leaped through the air, often repeatedly, in what appeared to be her vigorous efforts to elude the pursuing male. Only once was the actual spawning act observed, but at such close range and under such conditions of illumination that the details of movement could be closely followed: a pair upon coming to comparative rest near the surface, glided downward, counter-current, toward the bottom, moving side by side, frequently bringing their ventral surfaces into contact by a lateral turning of the body; before reaching the bottom the pair separated, each fish rapidly swimming away, although apparently not disturbed by the observer. The main feature of the breeding behavior of this fish, as outlined above, resemble those of other fresh-water fishes which have been studied, as for example the common northern species of Catostomidae, lately admirably described by Professor Jacob Reighard,[29] the major differences being largely paralleled by general differences in swimming habits.

LIFE-HISTORY

8. THE EGG.—Presumably extruded, as just indicated, considerably above the bottom, the egg of *Labidesthes sicculus* sinks very slowly in the water (as indicated by experiment). It is well supplied with a number of oil globules and with a flotation organ in the form of a filament many times

[27] In the water the males, with some exceptions, were readily distinguished by their deeper pigmentation; other secondary differences were not discovered in the measurement of a small series (marked sexual dimorphism in fishes outside of the Poeciliidae, seems generally confined to bottom-inhabiting forms).

[28] Spurious breeding behavior following incorrect sex-recognition was probably observed, but not critically studied.

[29] Biol Bull., 38, 1920, pp. 1–32.

longer than the diameter of the egg,[30] and thus must be transported for some distance by the water currents. The main function of this greatly elongated filament appears, however, to be that of fixation, for it is extremely adhesive while the egg itself is not. Doubtless after extrusion the egg adheres to the first object with which it comes into contact: in the spawning area most closely observed, this object would necessarily be a grain of current-washed gravel; in other areas, it would be some plant in the submerged vegetation. The only developing eggs actually secured were found by my assistant, Mr. Lyle S. Hubbard, on June 30 and July 1, on the stems of bulrushes near the bottom, in water about one meter deep on a wide marl shoal of Portage Lake where the rushes formed a thin patch.

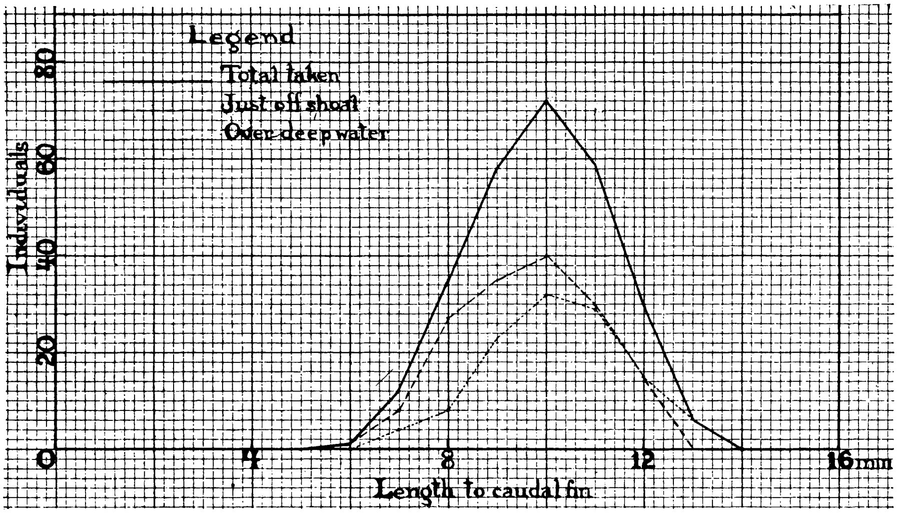

FIG. 2. Lengths to nearest millimeter of young-of-year *Labidesthes sicculus* taken June 26, 1920, in Portage Lake.

9. RATE OF DEVELOPMENT OF THE YOUNG.—Extremes of length of the young-of-the-year of *Labidesthes sicculus* were obtained on ten different days from June 24 to August 2 for computing the initial rate of growth. The data are plotted on the graph reproduced as figure 3. That the mode

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[30] In the ovary this filament is wound in a zig-zag spiral about the surface of the ovum, apparently in the position of its formation from the egg-membrane. The eggs of certain other free-swimming fishes are provided with a polar cluster of filaments; in the family (Atherinidae) to which Labidesthes belongs, they have been described for the genus Atherina in Europe and in South Africa, and for the genera *Menidia* and *Membras* of the east coast of the United States; but they are not developed on the ova of the Californian atherine genus Leuresthes, which possesses extremely highly specialized surf-breeding habits, described in excellent detail by Mr. Will F. Thompson (Fish Bull., Cal. Fish and Game Comm., no. 3, 1919, pp. 1–29).

of variation is not far from the mean, and that samples obtained near the edge of the shoals and over deep water near the center of the lake did not vary greatly (though slightly and significantly) in size, is indicated by the detailed measurements of the series collected on one of these ten days (see figure 2). At first the growth proved very rapid, about one millimeter increase per day in average size being indicated during the last week in June; then, however, a marked decrease in rate occurred, indicated on the graph as a sharp deflection in the growth curve,—presumably not a normal event in the life cycle since it is correlated with an abrupt fall in the temperature of the water at this time (see figure 1). The growth curve for the young-of-the-year of several other fishes measured at the same time and place show a like deflection. For thirty days following June 26, when a large series was measured (figure 2), the average size increment is 0.40 mm. per day (see figure 3). More or less definitely comparable data—being obtained at the same lake and during the same season—for fourteen species of which the young develop on the shoals, show that a distinctly higher rate of growth holds for these species than for the limnetic young of *Labidesthes sicculus;* only the minute darters grew more slowly. The data are presented below in tabular form.

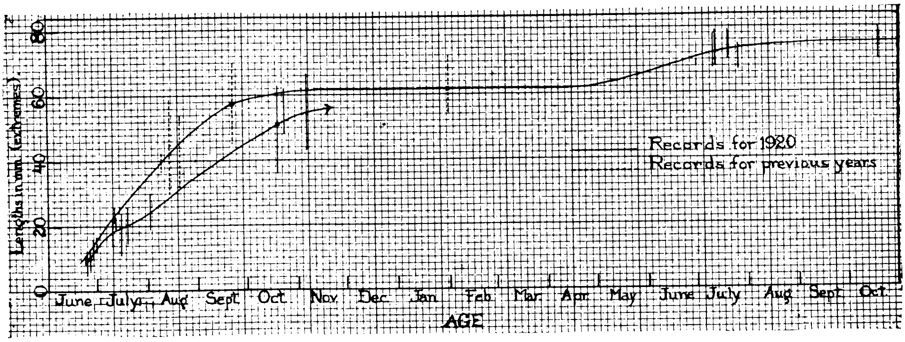

FIG. 3. Growth curve for *Labidesthes sicculus.*

*Table showing the estimated growth per day, for a thirty-day period early in the first summer's existence, for fourteen species of fresh-water fishes.**

Species	Daily growth	Species	Daily growth
Poecilichthys iowae	0.30 mm.	*Erimyzon sucetta*	0.50 mm.
Hadropterus aspro	0.31	*Micropterus dolomieu*	0.53
Boleosoma nigrum	0.34	*Micropterus salmoides*	0.57
Percina caprodes	0.40	*Ameiurus natalis*	0.60
Notropis cornutus	0.45	*Perca flavescens*	0.63
Pimephales notatus	0.48	*Esox vermiculatus*	0.96
Notropis hudsonius	0.50	*Lepisosteus osseus*	2.33

* Data all secured by the writer at Portage Lake, in Washtenaw and Livingston counties, Michigan, during the summer of 1920, which was below the normal in temperature (cf. figure 1).

The preceding table suggests several interesting possibilities, such as the similar rate of growth of related species; but generalization should await the accumulation of fuller data on these species, and of data on other species. It seems safe to assert on the basis of the evidence already obtained, however, that those species which attain a small adult size grow slowly during their first summer, whereas those which reach a large size, grow faster at first. The order of species as given in the table is, with irregularities, that of the average size of the adults. But this initial rate of growth is by no means directly proportionate to the adult size, for if the average growth increment per day as given be divided by the average adult size, a series of approximately constant values is not obtained; on the contrary, the series of species with added irregularities, is substantially inverted, a fact signifying that the smallest species grow fastest in reference to their final adult size. The data consequently seem to indicate that the small size of the smaller fishes studied results from the additive operation of two factors: the slower initial rate of growth, and a reduced period of vigorous growth, *i.e.*, hastened maturity. Evidence obtained by the writer in 1920 indicates that all of the fishes listed in the table with the exception of the darters and possibly *Esox vermiculatus,* pass through two or three years of immaturity, while the darters become mature at the age of one year; that the same condition holds for *Labidesthes sicculus* is proven in the following section.

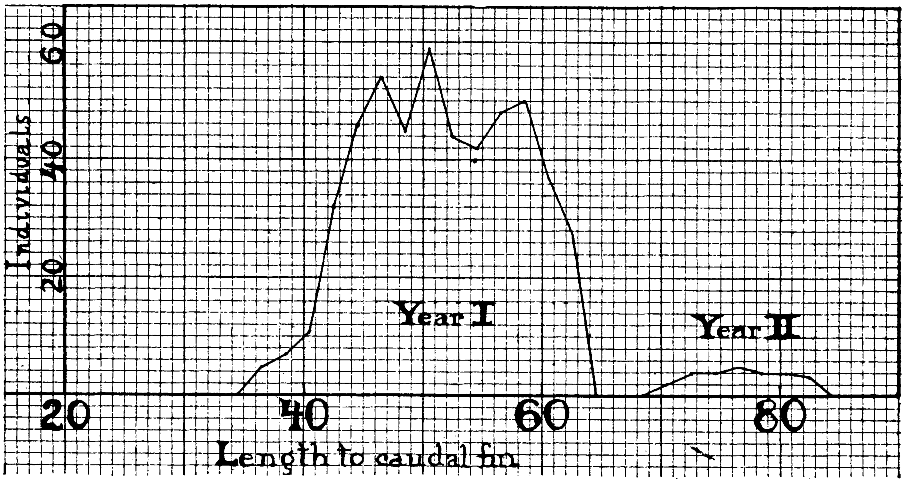

FIG. 4. Lengths (2 mm. frequency) of all *Labidesthes sicculus* taken on October 19, 1920, in Whitmore Lake, Washtenaw County, Michigan.

10. Life-cycle.—Length data obtained from series collected in 1920 and previous years in lakes of southern Michigan and along the shores of Lake Erie, plotted on a graph (figure 3) show, as indicated above, that the

growth rate of young *Labidesthes sicculus* was lowered during the summer of 1920 by a fall in the temperature during July, that normally the initial rapid growth is continued with a slight retardation throughout the months of July, August, and September, and that by their first autumn when only three or four months old, the young Labidesthes attain 0.7 to 0.8 their adult size (see figures 3 and 4). Within a month after hatching, in fact, the ova are already considerably enlarged. Only one annulus or winter mark is evident on the scales of the breeding fishes taken in the summer and autumn of 1920. This annulus, which obviously represents the scale margin during the long period of cessation of growth during the winter, is located a short distance within the margin of the scale. Since the exact distance is proportionate to the spring growth, the scales of fishes growing at approximately the same rate as the fish itself, the preceding winter's length was computed for the fishes taken in the summer of 1920 and entered on the accompanying graph (figure 3). That *Labidesthes sicculus* breeds at the age of one year consequently admits of no possible doubt. The fact that the adults are remarkably uniform in size,[31] that they have attained the full adult size accredited to the species, that none of the hundreds seen but not collected were notably larger (or smaller), that the immature ova of the mature females obtained were generally few and larger than those of the females taken in the first fall, that only mature rather than spent females were taken after the height of the breeding season, that one adult fish was found dead on shore in August, that only 4.2 percent of the 520 fishes obtained on the shoals of Whitmore Lake on October 19 were adult fishes, and finally that but one winter mark was evident on the scales of even the largest females secured—considering always that strictly determinate growth is an unknown phenomenon in fishes—all suggest the conclusion that *Labidesthes sicculus* is a fish characterized by an annual life-cycle, breeding but once at the age of one year, then dying and leaving the young-of-the-year as the only link over the winter connecting the generation of one year with that of the next.[32]

SUMMARY

This paper deals with the life history and ecology of *Labidesthes sicculus,* a fresh-water fish representative of the marine family Atherinidae. The very young occur chiefly over the deep water of lakes, while the adults are confined to shoal waters. Neither such physical factors as temperature, light, dissolved oxygen, nor food, appear to be involved in the determination of this complementary distribution; seclusion from enemies may be fundamentally but not immediately involved. The immediate cause appears to be a strong negative response to solid objects.

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[31] The decreased absolute as well as relative variation in size characteristic of the adults indicates that the principle of growth compensation, first demonstrated by Gilbert in the case of the Pacific salmon, holds in the case of Labidesthes (see Gilbert, Rept. Comm. Fish. Brit. Col., 1913 (1914), pp. 53-78, and also Hubbs, Biol. Bull., Vol. 40; pp. 206-208, 1921).

[32] The writer is not aware that an annual life-cycle has been demonstrated as holding for any fish, though suggested in the case of those remarkable neotenic anadromous fishes of China and Japan—the Salangidae.

During daylight the adults swim about near the surface and frequently leap through the air for short distances. During the night they lie quiescent against the surface. The very young swim about with their flattened heads in persistent contact with the surface film. Like many other fishes, these young congregate in schools only during the day.

Many of the form and color characters of Labidesthes are intimately correlated with its swimming habits. Its alimentary structures are correlated with its food.

Breeding occurs when the water is heated above 20° C. Moderate current over a washed bottom seems to be preferred as a breeding situation, though not invariably adopted. Each male guards an ill-defined surface area of water. Males predominate in numbers in the breeding areas, and usually more than one gives chase through both water and air to each entering female, a pair finally coming to rest and probably spawning in midwater.

The egg upon extrusion sinks very slowly, and adheres by an extremely long polar filament to the first object with which it comes in contact. The young after hatching increase first at the rate of about one millimeter per day, but appear to grow more slowly than do the young of other species, developing on the shoals. Within one month of hatching the ova are considerably enlarged; by winter about three fourths the adult size is attained; during winter there occurs a cessation of growth. Labidesthes breeds at the age of one year, and probably dies before its second winter, leaving the young-of-the-year as the only link connecting the generation of one year with that of the next.